

How well do we understand the impacts of alien species on ecosystem services?

A pan-European, cross-taxa assessment

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Recent comprehensive data provided through the DAISIE project (www.europe-aliens.org) have facilitated the development of the first pan-European assessment of the impacts of alien plants, vertebrates, and invertebrates – in terrestrial, freshwater, and marine environments – on ecosystem services. There are 1094 species with documented ecological impacts and 1347 with economic impacts. The two taxonomic groups with the most species causing impacts are terrestrial invertebrates and terrestrial plants. The North Sea is the maritime region that suffers the most impacts. Across taxa and regions, ecological and economic impacts are highly correlated. Terrestrial invertebrates create greater economic impacts than ecological impacts, while the reverse is true for terrestrial plants. Alien species from all taxonomic groups affect “supporting”, “provisioning”, “regulating”, and “cultural” services and interfere with human well-being. Terrestrial vertebrates are responsible for the greatest range of impacts, and these are widely distributed across Europe. Here, we present a review of the financial costs, as the first step toward calculating an estimate of the economic consequences of alien species in Europe.

Biological invasions complicate the conservation of biodiversity and ecosystem integrity worldwide. Invasive species can threaten biological diversity in various ways, from reducing genetic variation and eroding

gene pools, through the extinction of endemic species, and by altering habitat and ecosystem functioning (Hulme 2007; Table 1). Biological invasions also cause economic impacts that can be valued as financial costs, based on expert extrapolations of high-profile alien pests (Pimentel *et al.* 2001, 2005; Born *et al.* 2005; Collautti *et al.* 2006; Olson 2006; Lovell *et al.* 2006).

However, ecological and economic impacts of invasions are rarely compared within or between either geographic regions or taxonomic groups. Thus, even with increasing information, we still do not know the extent to which these impacts are correlated, how taxonomic groups differ in their impacts, and which biomes suffer most. This information is essential for prioritizing management actions.

Biological invasions have subtle socioeconomic consequences, which are difficult to assess using traditional monetary approaches and market-based models (Binimelis *et al.* 2007). To address this added complexity, we analyzed impacts described in the Millennium Ecosystem Assessment framework (MA 2005), in order to link ecological and economic impacts, by assuming that the effect of any ecological change influences ecosystem services and, in turn, human well-being. The ecosystem services approach attributes values to ecosystem processes, as the basis for all human needs. Ecosystem services are classified into four categories: “supporting” (ie major ecosystem resources and energy cycles), “provisioning” (ie production of goods), “regulating” (ie maintenance of ecosystem processes), and “cultural” (ie non-material benefits). The ecosystem assessment approach requires multidisciplinary collaboration in environmental management (Meyerson

In a nutshell:

- Ecological and economic impacts of alien species are usually studied separately, but they are likely to be highly correlated
- Few studies have compared these impacts, so their effects are probably underestimated for species-rich taxa or across large regions
- Although aliens may affect all categories of ecosystem services, current economic valuations focus primarily on “provisioning” services, because of limited available data relating to impacts on other services
- Nature conservation, agriculture, forestry, and fisheries are the main economic sectors where alien species cause marked direct costs in Europe
- Europe has the most up-to-date information on numbers of aliens and their impacts, but lags behind North America with respect to current knowledge of mechanisms underlying impacts; researchers from both continents can profit from each other's experiences and work toward reliable and comparable estimates of costs from alien species invasions

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Table 1. Percentage of publications from Europe and North America in global reviews of ecological impacts of alien species

Reference	Taxonomic group	Impact types	No. of publications	Europe	North America
Desprez-Loustau <i>et al.</i> (2007)	Fungus	R4; S1, 3; P2	77	28.57	58.44
Vilà <i>et al.</i> (2000)	Plants	P3	20	35.00	45.00
Ehrenfeld (2003)	Plants	S1–3, 5	77	10.39	50.65
Vilà <i>et al.</i> (2004)	Plants	P1	29	6.90	82.76
Levine <i>et al.</i> (2003)	Plants	S2–3; P2; R2, 5, 7, 9	152	6.58	57.89
Liao <i>et al.</i> (2007)	Plants	S1–2, 5	88	20.45	60.23
D'Antonio <i>et al.</i> (1999)	Terrestrial plants, vertebrates	S1; R8–10	52	0.00	50.00
Traveset and Richardson (2006)	Terrestrial plants, insects, vertebrates	P2; R1–2	38	26.32	10.53
Kenis <i>et al.</i> (2008)	Insects	S1–3; P2–3; R2–4, 9	403	5.21	62.28
Long (2003)	Mammals	S; P1–3; R1, 4, 6–9	339	30.97	20.35
Ciruna <i>et al.</i> (2004)	Freshwater species	P2; S1, 3; R3, 9; C1	94	22.34	43.62
Grosholz (2002)	Marine species	S3, 5; P3; R1, 3–4	31	0.00	93.55

Notes: See Figure 3 for “Impact types” code.

et al. 2005). Yet, a thorough, continent-wide analysis of the impacts of alien species on ecosystem services has not been completed; this would require the integration of data with information on the taxonomic identity and distribution of the species concerned (Crall *et al.* 2006).

Here, we provide the most comprehensive review of the ecological and economic impacts caused by alien species in Europe, based on data generated by the European Union (EU)-funded DAISIE (Delivering Alien Invasive Species Inventories for Europe; Panel 1) project. The results represent the first continent-wide assessment of impacts on ecosystem services by all major alien taxa – plants, vertebrates, and invertebrates – in terrestrial, freshwater, and marine environments. Our aims are to (1) estimate the number of alien species known to have ecological and/or economic impacts in Europe, (2) identify the most widespread species causing impacts and those with the broadest spectra of impacts, and (3) summarize available information on the financial costs of alien species in Europe.

■ General trends

Ecological and economic impacts

There are over 10 000 species alien to Europe registered in the DAISIE database (Panel 1), and yet ecological impacts are only documented for 1094 (11% of the total) of these species and economic impacts for only 1347 (13%) species. Not surprisingly, the most species-rich taxa (terrestrial invertebrates and terrestrial plants) contain the most species with recorded impacts. Thus, although absolute numbers may not be informative, examination of proportions reveals terrestrial vertebrates and freshwater organisms to be of particular concern, with more than one-third of registered species known to cause impacts (Table 2). The North Sea is the marine region with the highest number of alien species associated with ecological and economic impacts in Europe; this basin, together with the smaller marine basins, such as the Baltic and Black

Panel 1. The DAISIE project (www.europe-aliens.org)

DAISIE (Delivering Alien Invasive Species Inventories for Europe) was funded by the European Commission (2005–2008) to create an inventory of alien species that threaten European terrestrial, freshwater, and marine environments, in order to understand the environmental, economic, social, and other factors involved in alien invasions (Hulme *et al.* 2009a). The project was carried out by an international team of the leading experts in the field of biological invasions and an extensive network of European collaborators and stakeholders. In addition to collating one of the most comprehensive databases worldwide on introduced species, DAISIE aimed to raise awareness by producing factsheets on 100 of the “worst” European invasive species, as well as to mobilize researchers through a European registry of expertise in invasions.

The DAISIE database has collated information for fungi, plants, vertebrates, and invertebrates (including terrestrial, marine, and freshwater species) from up to 63 countries/regions (including islands) and 39 coastal and marine areas in both Europe and adjacent regions. Over 248 datasets, constituting more than 45 000 records on individual species alien to (ie native outside of Europe) or alien in (ie all aliens, including those that are native to somewhere else in Europe) Europe were assembled and verified by experts. This represents the largest database of alien species in the world. The database includes information on both the ecological and economic impacts of alien species in particular regions, documented not only by scientific journals and books, but also through the exploration of gray literature, local journals and books, and checklists written in languages other than English. The major findings, factsheets, and species list are summarized in DAISIE (2009).

The DAISIE database follows the classification of species based on invasion status proposed by Occhipinti-Ambrogi and Galil (2004) and Pyšek *et al.* (2004). Alien species are those introduced by humans that colonize outside their natural range and dispersal potential, whereas invasive species are those alien species that spread over a large area and attain high local abundances. The DAISIE database includes only alien species introduced after the discovery of America by Columbus in 1492.

Seas, harbor the highest proportions of species (Table 3). Although, overall, more species cause impacts in marine than freshwater ecosystems, marine species represent a smaller proportion of all alien species recorded.

Despite the fact that impacts of species belonging to “smaller” taxonomic groups (ie those containing relatively fewer species, such as terrestrial vertebrates and freshwater invertebrates) may be better studied than those in “larger” groups (such as terrestrial plants and terrestrial invertebrates, with two orders of magnitude more species), the greater proportional impacts may be attributable to more than simply an effect of sampling bias. One reason for this is the preponderance of predatory or omnivorous taxa among alien vertebrates and aquatic invertebrates. The introduction of vertebrate predators has been the primary cause of extinction globally, especially on islands (Blackburn *et al.* 2004), as well as the cause of cascading effects on trophic levels in freshwater ecosystems. Freshwater ecosystems are more vulnerable to introduced predators than are terrestrial and marine ecosystems, because native organisms generally have fewer defense mechanisms and greater naïveté toward novel predators (Cox and Lima 2006).

In general, more species are known to cause economic than ecological impacts, because the former are more easily perceived and are immediately reported by stakeholders. Economic pests are also likely to attract more scientific attention. For example, the Argentine ant (*Linepithema humile*) is one of the most studied alien organisms (Pyšek *et al.* 2008) and has been the subject of 14% of published studies on the impact of alien insects worldwide (Kenis *et al.* 2008).

Across the different regions in Europe (ie individual countries, major islands, or administrative units), there is a significant positive relationship between the number of species with ecological impacts and those with economic impacts (Figure 1). Among vertebrates and aquatic species, the number of species with ecological and economic impacts are more or less similar. In contrast, for terrestrial invertebrates, more species are known to cause economic than ecological impacts. Many introduced insects cause damage to agriculture or forestry, sectors with well-developed methods for estimating damage. For plants, the reverse is true, with ecological effects being more frequently documented than economic effects, even though the former are less tangible and cannot be estimated as market-based costs (Figure 1).

Most widespread species causing impacts

The taxonomic groups with impacts documented across the greatest number of regions in Europe are terrestrial vertebrates and terres-

Table 2. Total number and percentage of alien species known to have an ecological or economic impact for different taxonomic groups in Europe*

Taxonomic group	Total	Ecological impact (%)	Economic impact (%)
Terrestrial plants	5789	326 (5.6)	315 (5.4)
Terrestrial invertebrates	2481	342 (13.8)	601 (24.2)
Terrestrial vertebrates	358	109 (30.4)	138 (38.5)
Freshwater flora and fauna	481	145 (30.1)	117 (24.3)
Marine flora and fauna	1071	172 (16.1)	176 (16.4)

*DAISIE database search at 12 Feb 2008

trial invertebrates (Figure 2). For example, the muskrat (*Ondatra zibethicus*) and the racoon dog (*Nyctereutes procyonoides*) are known to cause problems in more than 50 European regions. Several insect species, such as the thrips *Frankliniella occidentalis* and *Heliothrips haemorrhoidalis*, are known to damage crops in more than 30 regions. The most widespread detrimental aquatic organisms are crustaceans, such as the Chinese mitten crab (*Eriocheir sinensis*, 20 regions), and mollusks such as the zebra mussel (*Dreissena polymorpha*, 20 regions) and the Pacific oyster (*Crassostrea gigas*, 18 regions). In contrast, alien terrestrial plants with known impacts are not usually widespread (Lambdon *et al.* 2008), and are often restricted to just one region (Figure 2). This finding illustrates that the perception of the consequences of invasion can be quite localized. Tree of heaven (*Ailanthus altissima*), black locust (*Robinia pseudoacacia*), and Japanese knotweed (*Fallopia japonica*) are the plant species with the most widespread impacts.

Which species are more widespread – those with economic or ecological impacts? There is no difference within terrestrial vertebrates and within aquatic taxa, but among the terrestrial invertebrates, those with economic impacts are more widespread, while for terrestrial plants it is species with ecological impacts that are more widespread (Figure 2).

■ Many impacts on ecosystem services

Using a representative list of 100 of the “worst” European invasive species, as designated by DAISIE (Panel 1), we classified taxa in relation to different types of impacts on the four main ecosystem services (Figure 3): supporting

Table 3. Total number and percentage of marine alien species having an ecological and economic impact by marine basin in Europe*

Basins	Area (km ²)	Total	Ecological impacts (%)	Economic impacts (%)
European Atlantic Ocean	3 700 000	359	66 (18.4)	80 (22.3)
Azov Sea	37 555	8	0 (0)	0 (0)
Baltic Sea	377 000	112	48 (42.9)	38 (33.9)
Barents Sea	1 400 000	2	1 (50)	0 (0)
Black Sea	436 400	23	12 (52.2)	11 (47.8)
Caspian Sea	371 000	24	0 (0)	0 (0)
Mediterranean Sea	2 500 000	501	47 (9.4)	30 (6.0)
North Sea	570 000	355	123 (34.6)	131 (36.9)

*DAISIE database search at 12 Sep 2008

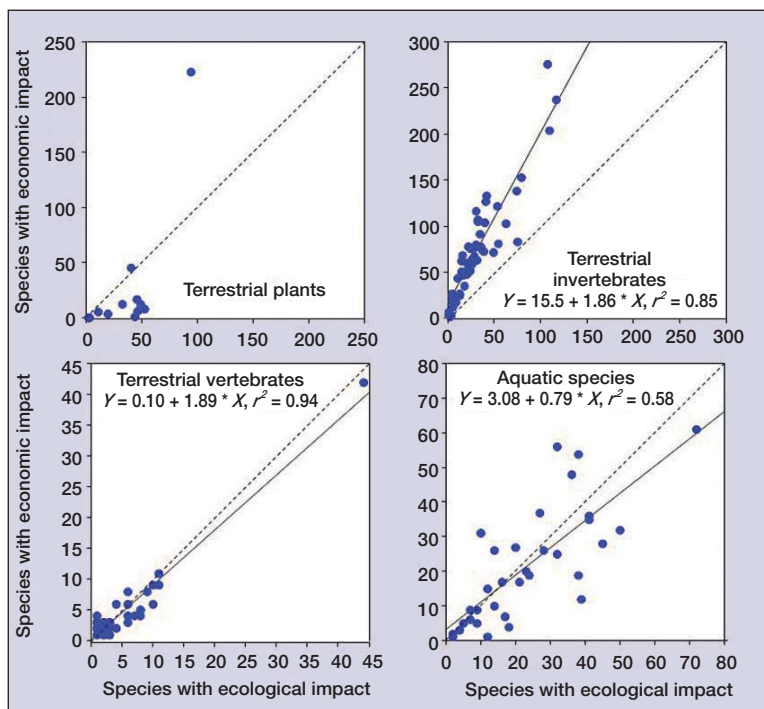


Figure 1. Relationship between the number of alien species with ecological and economic impact per region for different taxonomic groups in Europe. Each data point represents an individual country, major island, or administrative unit ($n = 63$). The outlier in terrestrial plants and vertebrates represents the United Kingdom. The linear regression for plants is not shown. Dashed line represents the line of unity. Data from the DAISIE database (see Panel 1).

(five types of impacts), provisioning (three types), regulating (ten types), and cultural (four types). As might be expected, a single invader can affect several different ecosystem services (Binimelis *et al.* 2007).

There are significant differences between taxonomic groups regarding the number of ecosystem services and different impact types caused by alien species (Figure 4). Terrestrial vertebrates exhibit the widest, and terrestrial invertebrates the narrowest, range of different impact types (Figure 4). The coypu (*Myocastor coypus*) best exemplifies the widespread damage that terrestrial verte-

brates can cause: these rodents damage crops, greatly disturb riverine vegetation by grazing, undermine riverbanks by burrowing, and transmit the bacterial disease leptospirosis (Bertolino and Genovesi 2007).

Aquatic invaders also exhibit a large number of different impact types per species (Table 4), with nine each reported for American crayfish (*Procambarus clarkii*), zebra mussel (*D. polymorpha*), and brook trout (*Salvelinus fontinalis*). In invaded temperate freshwater ecosystems, introduced crayfish represent the largest invertebrates and, being omnivores, they cause cascading effects on food webs. In addition, the diets of many vertebrates now depend upon the crayfish, which completely changes the trophic structure of the invaded community (Gherardi 2007). As in other parts of the world, zebra mussels modify supporting, regulating, and, ultimately, provisioning services in aquatic ecosystems, through alteration of water quality and bioaccumulation. Brook trout, which have been introduced into more than 20 European countries for sport fishing, affect all four main ecosystem service categories, as well as altering populations of native salmonids through hybridization and reduction in numbers of other freshwater taxa. They also change primary production and benthic resource patterns of formerly oligotrophic lakes.

In summary, it appears that alien taxa often have several different types of impacts, rarely restricted to a single ecosystem service. There is a positive correlation between the number of impacts and the number of services affected by alien species ($r^2 = 0.60$, $P < 0.0001$).

■ Financial costs to ecosystem services

Even though some invaders have clear economic impacts, only a handful of cost–benefit analyses have been applied to aliens in Europe, and there have been only a few cross-

Table 4. The top 10 invasive species identified by DAISIE (Panel 1), with the highest number of different impact types on ecosystem services in Europe

Species	Taxonomic group	Impact types	Native range
<i>Oxalis pes-caprae</i>	Terrestrial plant	2P, 4R, 2C	South Africa
<i>Branta canadensis</i>	Terrestrial vertebrate	2S, 2P, 2R, 2C	Nearctic North America
<i>Cervus nippon</i>	Terrestrial vertebrate	3S, 1P, 3R, 2C	East Asia
<i>Myocastor coypus</i>	Terrestrial vertebrate	3S, 1P, 3R, 2C	South America
<i>Dreissena polymorpha</i>	Freshwater invertebrate	1R, 1P, 4R, 3C	Black, Caspian, and Aral Seas
<i>Procambarus clarkii</i>	Freshwater invertebrate	1S, 2P, 5R, 1C	Mexico and South-central USA
<i>Salvelinus fontinalis</i>	Freshwater vertebrate	3S, 3P, 1R, 2C	North America
<i>Codium fragile</i>	Marine alga	3S, 1P, 4R	Japan
<i>Undaria pinnatifida</i>	Marine alga	2S, 2P, 4R	Northwest Pacific
<i>Balanus improvisus</i>	Marine invertebrate	1S, 1P, 6R	Atlantic

Notes: The number of impacts is indicated by S: supporting, P: provisioning, R: regulating, and C: cultural services. See Figure 3 for “Impact types” code.

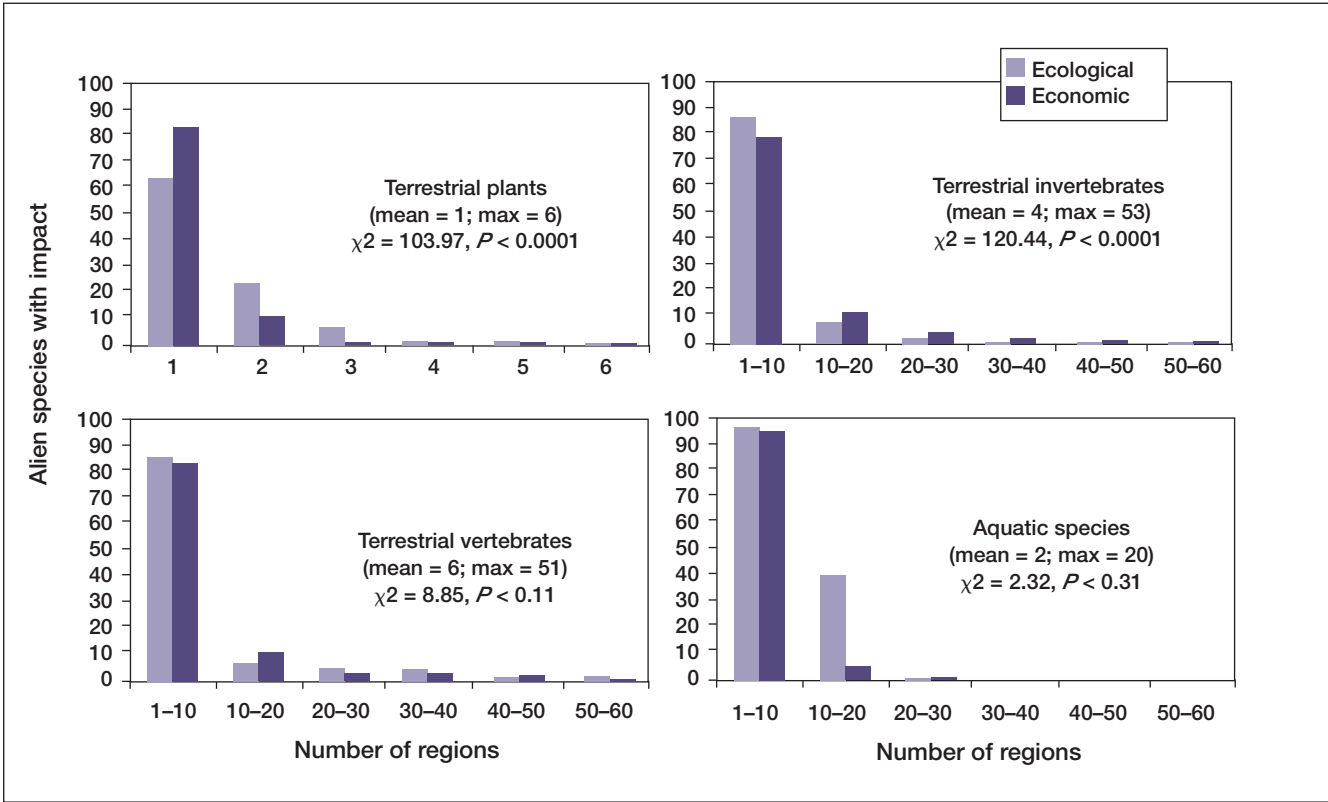


Figure 2. Frequency distribution of alien species with ecological and economic impacts in Europe. Significant differences between the distribution of species with ecological and economic impacts are indicated by chi-squared tests. The mean and maximum number of regions per taxonomic group are given in parentheses. Data from the DAISIE database (see Panel 1).

taxa cost estimates at the national level. There have been no cost estimates for very widespread and harmful invaders across the whole of Europe. This perspective differs from that in North America (Panel 2). In Europe, most expenses generated by invaders are in the form of

management costs, including eradication, control, monitoring, and environmental education programs targeting emblematic natural areas for which there was specific funding. For example, the over 100 Financing Instrument for the Environment (LIFE) programs aimed at eradicat-

Panel 2. Lessons from – and for – North America

There are at least 1000 scientific case studies published on the impact of invasive species on one or more ecosystem services (Table 1). While 53% of the studies have been conducted in North America, the similarly sized continent of Europe contributes only 16%. These published studies are essential to understanding the ecological mechanisms underlying the impacts of invasive species. However, to translate the ecological information into monetary terms for individual continents, it is necessary to know the number of alien species causing ecological and economic impacts. This is now well known for Europe, as a result of DAISIE, but (as yet) not for North America. Such an analysis requires a comprehensive assessment of the numbers of species that have become naturalized in North America and of the proportions that have resulted in economic or ecological impacts. The groundwork for such an assessment does exist, at least in the US. A total of 319 datasets on alien species, over half of which are available online, have been identified (Crall *et al.* 2006; Graham *et al.* 2008), and while the taxonomic composition, geographic distribution, and extent of additional information might be variable, this represents a promising platform from which to launch an initiative equivalent to DAISIE on the other side of the Atlantic.

Although DAISIE reflects the foresight of the European Commission in identifying the need for an inventory of alien species, Europe lags behind North America in the direct quantification of financial impacts. For example, the publication of *Harmful non-indigenous species in the United States* (OTA 1993) played a pivotal role in raising awareness of the ecological and economic impacts of biological invasions. This document reported US\$97 billion in damages from 79 alien species during the period from 1906 to 1991. This value has subsequently been updated to US\$120 billion per year (Pimentel *et al.* 2005), following the inclusion of additional species. In Canada, the projected costs of 111 invasive species to fisheries, agriculture, and forestry have been estimated to be CDN\$13–34 billion per year (Colautti *et al.* 2006). Financial costs across regions are difficult to compare (Born *et al.* 2005), especially if different sectors are examined. This explains the differences between the estimates in the US and Canada, where the higher value in the former reflects the inclusion of feral domestic animals and human diseases in the calculations. For Europe, DAISIE has identified the financial costs of relevant plants and animals affecting nature conservation, agriculture, forestry, and fisheries (see Table 5 for some examples). From this, an overall European cost estimate is underway, for the development of an EU Strategy on Invasive Alien Species

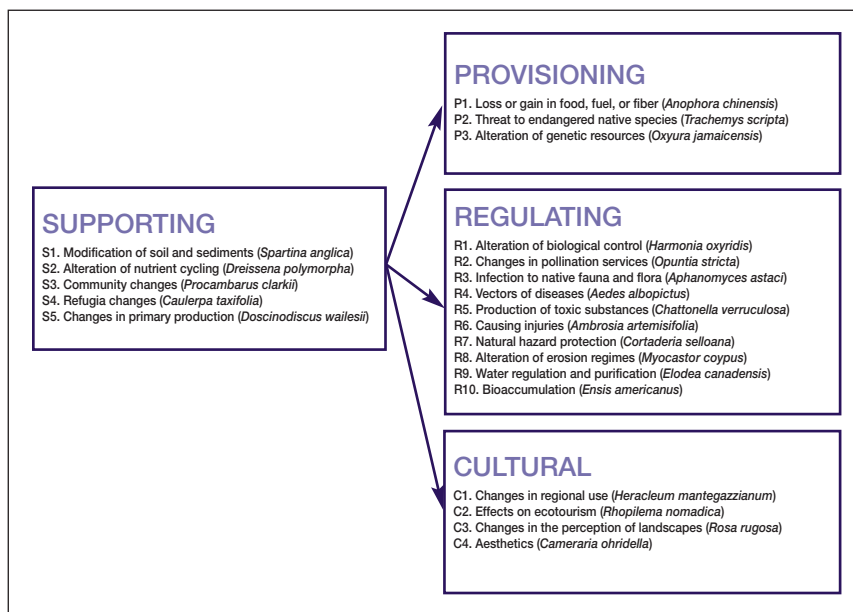


Figure 3. Examples of impact types of invasive species in Europe classified into four categories of ecosystem services, based on Binimelis et al. (2007).

ing alien vertebrates on islands to protect marine birds resulted in expenditures totaling in excess of €27 million (Scalera and Zaghi 2004). Expenditure has also gone toward controlling widespread invasive alien plants, such as the ice-plant (*Carpobrotus* spp) in the Mediterranean littoral zone and giant hogweed (*Heracleum mantegazzianum*)

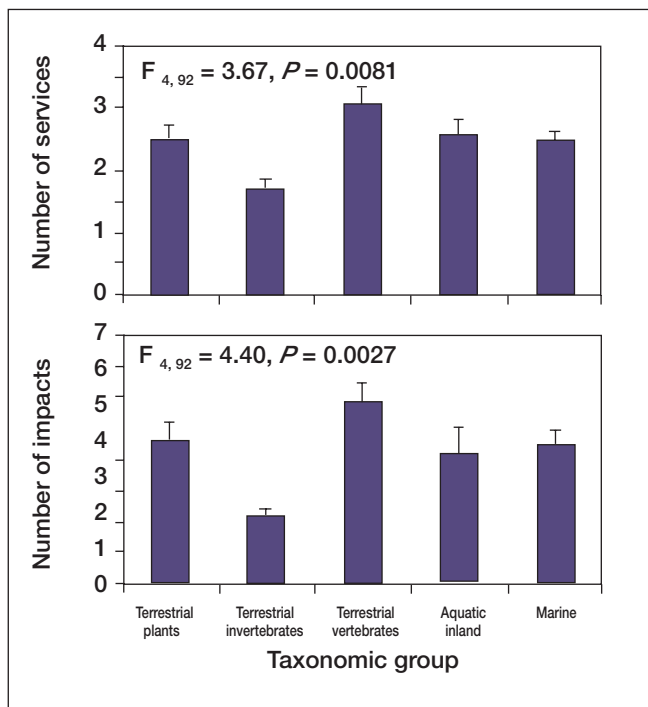


Figure 4. Average (+ SE) number of ecosystem services (ie supporting, provisioning, regulating, and cultural) and number of impacts affected by different taxonomic groups, based on information on 100 of the “worst” European invasive species (excluding the data for three fungal species). See Figure 3 for the types of impacts. Data from the DAISIE project (see Panel 1).

in temperate Europe (Table 5). Through extrapolation from herbicide sales, Williamson (2002) has estimated that the cost of chemical control for 30 alien weeds in the UK could be over €150 million per year.

In addition to management costs, information on losses to provisioning services is occasionally available, primarily for the agricultural, forestry, and fisheries sectors. In the UK, annual crop losses due to alien arthropods are estimated at €2800 million, which, together with damages inflicted by pathogens and vertebrates, adds up to €3800 million per year (Pimentel et al. 2001). In Germany, the estimated minimum costs of losses in stored grain – attributable to only three damaging arthropods – might be as high as €12 million per year (Reinhardt et al. 2003). In the region surrounding Milan, Italy, an attempt to

eradicate populations of an invasive Asian long-horned beetle (*Anoplophora chinensis*) resulted in the removal of 2000 trees, at a cost of €1.06 million, apparently without success (van der Gaag 2007). A cost–benefit analysis conducted in Italy has shown that even an active control plan for coypu (*Myocastor coypus*) over 5 years has not decreased costs arising from the damage it causes to agriculture and riverbanks (Panzacchi et al. 2007).

Marine fisheries highlight the complexity arising from both costs and benefits to provisioning services following the introduction of an alien species. For example, some Erythrean fishes (ie species from the Red Sea, introduced through the Suez Canal) have become part of the Levantine (eastern Mediterranean) fisheries (Galil et al. 2009), but others, such as the blue-spotted coronetfish (*Fistularia commersonii*), have a low market value themselves and prey on commercially important native Mediterranean fishes, such as the picarel (*Spicara smaris*) and bogue (*Boops boops*). However, few studies have estimated the costs of alien species to fisheries, and those estimates that do exist depend on the model assumptions. For instance, from the mid-1980s to the early 1990s, invasion by the combjelly (*Mnemiopsis leidyi*) contributed to 10% losses in commercial harvests of the anchovy (*Engraulis encrasicolus*) in the Black Sea. This decline is estimated at between €12.3 million (Knowler 2005) to €16.9 million per year (Travis 1993), depending on the underlying fisheries model used.

The introduction of crayfish is often assumed to contribute positively to local economies by developing new aquaculture opportunities, such as for farmed American crayfish in southern Spain (Gherardi 2007). An integral cost–benefit analysis of alien species in fisheries or aquaculture is lacking and would be complex to undertake. For example, commercial fisheries losses due to the Chinese



Figure 5. Invasive species in Europe causing a variety of impacts on ecosystem services include (a) American crayfish (*Procambarus clarkii*), (b) common slider (*Trachemys scripta elegans*), (c) prickly pear cactus (*Opuntia maxima*), and (d) muskrat (*Ondatra zibethicus*).

mitten crab may range from €73.4–€84.7 million since 1912, as a result of intermittent mass occurrences in German waters (Fladung pers comm). However, because the crabs are sold as food (amounting to sales of €3–€4.5 million between 1994 and 2004), this quantity needs to be deducted from impact costs arising from their burrowing activity, which erodes dikes and river and lake embankments (Gollasch and Rosenthal 2006; Gherardi 2007).

Finally, damage costs to aquatic infrastructures, especially due to fouling organisms, can be high. The great shipworm (*Teredo navalis*), a bivalve, has destroyed dikes and flood protection installations in the Baltic and North Seas (Leppäkoski *et al.* 2002). Similarly, damage by the Erythrean nomadic jellyfish (*Rhopilema nomadica*) to power plant intake pipes situated along the Levantine coast has cost €36 530 per year to repair (Galil and Zenetos 2002). Unfortunately, there are only a few published studies on actual or projected costs to individual countries or maritime basins for widely distributed aquatic invertebrates known to have high economic impacts.

The non-material benefits that people obtain from ecosystems are also influenced by alien species, but are

more difficult to quantify, because most of the evidence is anecdotal (Bardsley and Edwards-Jones 2006). Changes in the recreational use of natural areas or impacts on eco-tourism activities are often described, but not evaluated. In the 1970s, the nomadic jellyfish entered the Mediterranean Sea via the Suez Canal. Local municipalities along the Aegean and Levantine coastlines reported a subsequent decrease in the number of tourists frequenting the beaches, because of concerns over the painful stings this jellyfish can inflict (Galil and Zenetos 2002). In contrast, many alien plants are considered to be emblematic species in certain landscapes. On Danish beaches and sand dunes, the Japanese rose (*Rosa rugosa*) grows in such abundance that it forms thorny thickets that are impenetrable to beachgoers (Weidema 2006). Despite this nuisance, blooming thickets are displayed in tourist brochures and on postcards. In Mediterranean coastal areas, the Central American *Opuntia* and *Agave* species are typical floral elements and attract the attention of tourists looking for “Wild West” landscapes (Vilà 2008).

Many invaders cause health problems. Nearly 100 (~6%) of the alien invertebrate species in Europe

Table 5. Alien species in Europe generating some of the highest costs

Species	Biome/taxa	Country	Extent	Cost item	Period	Cost (million € year ⁻¹)	Reference
<i>Carpobrotus</i> spp	Terrestrial plant	Spain	Localities	Control/eradication	2002–2007	0.58	Andreu <i>et al.</i> (in press)
<i>Anoplophora chinensis</i>	Terrestrial invertebrate	Italy	Country	Control	2004–2008	0.53	Van der Gaag (2007)
<i>Cervus nippon</i>	Terrestrial vertebrate	Scotland	Localities	Control		0.82	White and Harris (2002)
<i>Myocastor coypus</i>	Terrestrial vertebrate	Italy	Localities	Control/damages	1995–2000	2.85	Panzacchi <i>et al.</i> 2007
<i>Sciurus carolinensis</i>	Terrestrial vertebrate	UK	Country	Control	1994–1995	0.46	White and Harris (2002)
<i>Azolla filiculoides</i>	Freshwater plant	Spain	Protected area	Control/eradication	2003	1.00	Andreu <i>et al.</i> (in press)
<i>Eichhornia crassipes</i>	Freshwater plant	Spain	River basin	Control/eradication	2005–2007	3.35	Andreu <i>et al.</i> (in press)
<i>Oxyura jamaicensis</i>	Freshwater vertebrate	UK	Country	Eradication	2007–2010	0.75	Scalera and Zaghi (2004)
<i>Chrysochromulina polylepis</i>	Marine algae	Norway	Country	Toxic bloom		8.18	Hopkins 2002
<i>Rhopilema nomadica</i>	Marine invertebrate	Israel	Coast	Infrastructure damage	2001	0.04	Galil and Zenetos (2002)

Notes: Values are actual expenditures and not estimates or extrapolations. See WebTable 1 for a full list of examples.

adversely affect human and animal health (Roques *et al.* 2009). Biting insects that can potentially transmit disease include seven mosquitoes and over 30 ectoparasites. More than half of the 47 introduced nematodes are endoparasites of humans or cause zoonoses (an infectious animal disease that can be transmitted to humans) in cattle and game animals. Some aliens that pose a health risk to humans live in or around buildings, including two recluse spiders (*Loxosceles* spp) from the Americas, the bites of which can lead to necrosis, and the venomous redback spider (*Latrodectus hasselti*) from Australia (Kobelt and Nentwig 2008). Several alien plants produce allergenic pollen and increase the prevalence of hay fever (Belmonte and Vilà 2004), whereas giant hogweed produces sap that causes skin lesions upon contact (Pyšek *et al.* 2007). The only available estimates of medical costs of European invaders are for the treatment of allergic reactions to ragweed pollen (*Ambrosia artemisiifolia*) in Germany (Reinhard *et al.* 2003).

Conclusions

Our survey has revealed that there are over 1000 alien species known to cause ecological or economic impacts in Europe. Although these findings reflect the current state of knowledge, they are likely to change as more information is gathered.

Many invaders cause multiple impacts over a large area in Europe. The overall impact depends upon their distribution, local abundance, and per capita effect (Parker *et al.* 1999), but these three components are difficult to quantify. An integrated database, such as that produced through DAISIE, enables the identification of the most widespread species causing impacts, as well as those with the widest range of impacts on ecosystem services. The Millennium Ecosystem Assessment approach – to quantify the services most at risk from invasive species – should help rank different species, and should also assist in prioritizing management procedures (Hulme 2006). This approach is a crucial first step toward finding indicators of ecosystem service disruption

(Meyerson *et al.* 2005); however, as yet, ecosystem services are still not well integrated into conservation assessments (Egoh *et al.* 2007).

The financial costs of invasions in Europe can be grouped by their detrimental effects on provisioning services and the actions required to manage alien species populations. Besides conservation, the sectors of agriculture, forestry, fisheries, and health seem to be the main economic sectors where alien species lead to substantial costs financially (Panel 2). Yet, the economic evaluation of alien species cannot be based solely on market-based costs; should be included indirect and non-use value costs as well (Born *et al.* 2005). These results, drawn from DAISIE, should establish a European benchmark, from which further research on impacts can develop. Given evidence of increasing numbers of alien species introductions to this region over the past few decades (Hulme *et al.* 2008), such assessments must become a regional priority.

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WebTable 1. Examples of monetary costs of alien species invading Europe

Species	Biome/taxa	Country	Extend	Cost item	Cost (million€ per year)	Reference
<i>Carpobrotus</i> spp	Terrestrial plant	Spain	Localities	Control/eradication	0.29	Andreu <i>et al.</i> (in press)
<i>Eucalyptus</i> spp	Terrestrial plant	Spain	Localities	Control/eradication	1.58	Andreu <i>et al.</i> (in press)
<i>Fallopia japonica</i>	Terrestrial plant	UK	Localities	Eradication	0.81	Child <i>et al.</i> (2001)
<i>F japonica</i> , <i>F bohemica</i> , <i>F sachalinensis</i>	Terrestrial plant	Czech Rep	Localities	Control/containment	0.02	Křivánek (2006)
<i>Heracleum mantegazzianum</i>	Terrestrial plant	Czech Rep	Localities	Control/containment	0.01	Křivánek (2006)
<i>H mantegazzianum</i>	Terrestrial plant	Denmark	Localities	Control	0.08	Nielsen <i>et al.</i> (2005)
<i>H mantegazzianum</i>	Terrestrial plant	UK	Country	Control	0.19	Shaw (2003)
<i>H mantegazzianum</i> , <i>F japonica</i> , <i>F bohemica</i> , <i>F sachalinensis</i> , <i>Impatiens glandulifera</i> , <i>Rudbeckia laciniata</i>	Terrestrial plant	Czech Rep	Localities	Control/containment	0.02	Křivánek (2006)
<i>Pennisetum setaceum</i>	Terrestrial plant	Spain	Localities	Control/eradication	0.62	Andreu <i>et al.</i> (in press)
<i>Pinus strobus</i> , <i>Larix decidua</i>	Terrestrial plant	Czech Rep	Protected area	Control/containment	0.05	Hentschel and Hentschelová (2003)
<i>Rhododendron ponticum</i>	Terrestrial plant	UK	Protected area	Control	66.26	Gritten (1995)
<i>Anoplophora chinensis</i>	Terrestrial invertebrate	Italy	Country	Control	0.53	van der Gaag (2007)
<i>Branta canadensis</i>	Terrestrial vertebrate	Germany	Country	Eutrophication	1.02	Gebhart (1996)
<i>Cervus nippon</i>	Terrestrial vertebrate	Scotland	Localities	Control	0.82	White and Harris (2002)
<i>Chrysolophus pictus</i>	Terrestrial vertebrate	Germany	Country	Damages	1.28	Gebhart (1996)
<i>Felis catus</i> , <i>Rattus</i> sp	Terrestrial vertebrate	Italy	Small islands	Eradication	0.19	Scalera and Zaghi (2004)
<i>F catus</i> , <i>Rattus</i> sp	Terrestrial vertebrate	France	Small islands	Eradication	0.21	Scalera and Zaghi (2004)
<i>F catus</i>	Terrestrial vertebrate	UK	Localities	Control	3.62	White and Harris (2002)
<i>Hystrix hodgsoni</i>	Terrestrial vertebrate	UK	Localities	Eradication	0.03	Smallshire and Davey (1989)
<i>Muntiacus reevesi</i>	Terrestrial vertebrate	UK	Localities	Control	0.02	White and Harris (2002)
<i>Mustela vison</i>	Terrestrial vertebrate	UK	Country	Eradication	0.55	Moore <i>et al.</i> (2003)
<i>M vison</i>	Terrestrial vertebrate	Estonia	Country	Eradication	0.12	Scalera and Zaghi (2004)
<i>Myocastor coypus</i>	Terrestrial vertebrate	UK	Country	Eradication	0.45	Gosling and Baker (1989)
<i>M coypus</i>	Terrestrial vertebrate	Italy	Localities	Riverbank damages	2.14	Panzacchi <i>et al.</i> (2007)
<i>M coypus</i>	Terrestrial vertebrate	Italy	Localities	Agricultural damages	0.19	Panzacchi <i>et al.</i> (2007)
<i>M coypus</i>	Terrestrial vertebrate	Italy	Localities	Control	0.52	Panzacchi <i>et al.</i> (2007)
<i>Oryctolagus cuniculus</i>	Terrestrial vertebrate	Germany	Country	Control	5.11	Gebhart (1996)
<i>O cuniculus</i>	Terrestrial vertebrate	UK	Localities	Control	41.18	White and Harris (2002)
<i>O cuniculus</i> , <i>Rattus</i> sp, <i>M coypus</i> , <i>M vison</i>	Terrestrial vertebrate	France	Small islands	Control/eradication	0.29	Scalera and Zaghi (2004)
<i>Lithobates catesbeianus</i>	Terrestrial vertebrate	UK	Locality	Eradication	0.01	Adrados and Briggs (2002)
<i>Rattus norvegicus</i>	Terrestrial vertebrate	UK	Small islands	Eradication	0.28	Scalera and Zaghi (2004)
<i>Sciurus carolinensis</i>	Terrestrial vertebrate	UK	Country	Control	0.46	White and Harris (2002)
<i>Azolla filiculoides</i>	Freshwater plant	Spain	Protected area	Control/eradication	1.00	Andreu <i>et al.</i> (in press)
<i>Crassula helmsii</i>	Freshwater plant	UK	Localities	Control	0.88	Shaw (2003)
<i>Eichhornia crassipes</i>	Freshwater plant	Spain	River basin	Control/eradication	3.35	Andreu <i>et al.</i> (in press)
<i>Dreissena polymorpha</i>	Freshwater invertebrate	Spain	River basin	Infrastructure and boat damage	2.00	Alonso (2006)
<i>Oxyura jamaicensis</i>	Freshwater vertebrate	Spain	Protected area	Eradication	0.06	Cevallos pers comm
<i>O jamaicensis</i>	Freshwater vertebrate	UK	Country	Eradication	0.75	Scalera and Zaghi (2004)
<i>Chattonella</i> spp	Marine algae	Norway	Country	Toxic bloom	7.43	Hopkins (2002)
<i>Chrysochromulina polylepis</i>	Marine algae	Norway	Country	Toxic bloom	8.18	Hopkins (2002)
<i>Cercopagis pengoi</i>	Marine invertebrate	Finland	Gulf	Decline in fish catches	0.02	Panov <i>et al.</i> (1999)
<i>Rhopilema nomadica</i>	Marine invertebrate	Israel	Coast	Infrastructure damage	0.04	Galil and Zenetos (2002)

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